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Equal temperature-size responses of the sexes are widespread in arthropod species

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AGH, CH and DA designed the study, wrote the paper and defined the statistical approaches. CH collected the data and performed the statistical analyses.

Abstract

Sexual size dimorphism (SSD) is often affected by environmental conditions, but the effect of temperature on SSD in ectotherms still requires rigorous investigation. We compared the plastic responses of size-at-maturity to temperature between males and females within 85 diverse arthropod species, in which individuals of both sexes were reared through ontogeny under identical conditions with excess food. We find that the sexes show similar relative (proportional) temperature-body size (T-S) responses on average. The high degree of similarity occurs despite an analysis which includes a wide range in animal body sizes, variation in degree of SSD, and differences in the sign of the T-S response. We find no support for Rensch's rule, which predicts greater variation in male size, or indeed the reverse, greater female size variation. SSD shows no systematic temperature dependence in any of the 17 arthropod orders examined, 5 of which (Diptera, Orthoptera, Lepidoptera, Coleoptera and Calanoida) include ≥6 thermal responses. We suggest that the same proportional T-S response may generally have equivalent fitness costs and benefits in both sexes. This contrasts with effects of juvenile density, and food quantity/quality, which commonly result in greater size plasticity in females, suggesting these variables have different adaptive effects on SSD.

Introduction

Difference in body size between males and females within a species is termed sexual size dimorphism (SSD), and is widely observed throughout the plant and animal kingdoms [1]. Male-biased SSD, where males are the larger sex, is common among endothermic vertebrates, and may in part relate to males competing for mates [2,3]. By contrast, female-biased SSD tends to predominate in ectothermic invertebrates and vertebrates [4,5]. The dimorphic niche hypothesis (reproductive role hypothesis) states that the differential reproductive roles of the sexes are associated with differential energetic costs [6] leading to different size optima [7,8], hence SSD. In most invertebrate species, there is considered to be selection for larger females, because this favours larger clutch size and / or offspring size. Males may benefit indirectly from a smaller body size associated with earlier adult emergence (protandry) because this may increase their chance to reach maturity (important when they rove for females and suffer high mortality risk), while in populations with discrete generations this may increase the potential of males to be ready to fertilize females that reach sexual maturity later [9-11].

Although SSD has at times been assumed to be rather invariant within a species, studies have found this to change as a consequence of significantly greater variation in size of males [12] or females [13]. A variety of rules and theories have been formulated to explain variation in SSD, both between and within species [14-16]. Rensch's rule (RR) states that male body size varies more than female body size, irrespective of which sex is larger. RR was originally formulated to describe the pattern seen across species within a related clade, but has since been tested within species to see if similar drivers exist at the intra-specific level [13,17]. Within a species it predicts an increase in SSD with increasing body size in species where males are the larger sex, and a decrease in SSD with body size in species where females are larger [14,16]. One prominent general hypothesis (i.e. evolutionary mechanism) potentially generating RR is when, over evolutionary time, directional (primarily

sexual) selection for large male size is overall stronger than directional (primarily fecundity) selection for large female size [4]. Additionally, the fitness consequences of large versus small body size can differ between the sexes under different ecological and environmental conditions because the sexes differ in the degree of plasticity they exhibit in response to climatic or ecological variables [17-19].

Variation in size at maturity has been widely documented for ectothermic species experiencing different thermal regimes during ontogeny [20-23]. This intra-specific phenotypically plastic response commonly leads to a reduction in size-at-stage with warming, and has been called the Temperature-Size Rule (TSR) [20]. Given the ubiquity of the TSR in taxonomic groups as diverse as bacteria, protists and metazoans [22,24,25], the proximate and ultimate causes have been explored in some detail [22,25-29]. The temperature-size (T-S) response has been shown to vary in magnitude in relation to species body size, voltinism, and taxonomic group, and between aquatic and terrestrial-living species [22,23]. Variation in SSD can result when males and females respond differently to their environment (differential-plasticity hypothesis [18]), and this may be an important contributor to the observed variation in SSD. Thus the degree to which different environmental factors such as juvenile density, food quality or quantity, and temperature elicit contrasting plastic body size responses between the sexes should be informative [12,19]. Here we specifically focus on sex-dependent differences in temperature-size (T-S) responses, as this may ultimately help to elucidate the underlying drivers of both SSD and T-S responses. Sex-based differences in T-S responses have been considered before; while most studies have been experimental and have considered single species, the syntheses and analyses of responses by Teder & Tammaru (2005) [13] and Stillwell *et al*. (2010) [19] on insects, have looked more broadly at differential changes in SSD with environmental conditions. We increase the amount of temperature response data considered by almost 4-fold in our analysis, and increase the range of species to include other Arthropoda. This allows greater power when testing variation in SSD with temperature. Furthermore, we explore variation in

absolute sexual size differences across temperatures, and for the first time the degree to which SSD relates to the magnitude of the T-S response.

Most analyses of variation in body size responses (and comparisons between the sexes) have expressed this change in relative terms, for example, using regressions to derive the slope of log size of one sex versus the other, or comparing SSD as a proportion (see the varied approaches in Stillwell & Fox [12]; Teder & Tammaru [13]; and Stillwell *et al*. [19]). The use of relative size responses allows for the removal of bias caused by the differences in body size of the sexes, and reduces statistical problems. Yet changes in absolute size differences between the sexes may hold important information relating to mate assessment and performance [30-32]. Consequently, although we focus our efforts mainly on exploring the thermal dependence of SSD within species using relative metrics, we also consider the implications of absolute differences in size between the sexes, and how this changes with temperature. We seek to test a range of interrelated questions using data from a diverse set of species from within the Arthropoda, specifically:

i. Do the T-S responses differ systematically between the sexes intra-specifically, and is there any evidence to support Rensch's rule?
ii. Do differences in the T-S responses of the sexes relate to the magnitude of sexual size dimorphism?
iii. How does the absolute difference in body mass between the sexes vary with temperature, and how does this differ from the relative responses?
iv. How does the effect of temperature on SSD compare with that of other environmental influences: food quantity and quality, pathogen infection, photoperiod and larval crowding and competition, as quantified by Stillwell et al. (2010) [19]?

Methods

The data compilation of Horne *et al*. [23] was revisited; this provides a single extensive set of data on the size-at-maturity responses to temperature of a wide range of arthropod species,

123 including marine, freshwater and terrestrial forms. Briefly, studies were systematically
124 screened to include only laboratory studies where individuals were reared at a range of
125 constant temperatures, with food concentrations at or above saturation, in order to remove
126 the confounding impact of food limitation. Extreme, potentially stressful temperatures were
127 excluded. Only adult size measurements were used for analysis from studies where males
128 and females had been separated. In a small minority of cases pupal size was considered to
129 be a reliable correlate of size at maturity. We were careful to ensure that we only included
130 measurements when data for both sexes had been provided and the same controlled
131 experimental conditions were used for each sex. The minimum period of acclimation for the
132 inclusion of adult size data was set so that only individuals that were raised from egg or first
133 larval stage were included. Adult data were collected as a variety of metrics including
134 lengths, volumes, and dry, wet or carbon mass. These measurements were subsequently
135 converted to dry mass (mg) using intra-specific regressions. Where these were not available,
136 regressions for closely related species, and occasionally more general inter-specific
137 regressions, were used. All data and conversions are detailed in our Table S1.
138
139 The sex-specific slopes of $\log_e$ dry mass vs. temperature were used to examine thermal
140 responses in body size for single species. This exponential form has the advantage of being
141 a better fit than alternate transformations, as judged by Akaike weights (see Table S2 in
142 Supplementary Information). Moreover, it has the distinct advantage of allowing examination
143 of relative change and is largely unbiased by absolute body size. We transformed the slopes
144 into percentage change in dry mass per ^{o}C, using the formula, $(\exp^{(slope)} -1)*100$ = % change
145 in mass per °C [22]. A negative percentage indicates a decrease in size with increasing
146 temperature (following the TSR) and a positive percentage an increase in size (converse-
147 TSR).
148
149 Differences in body size variation can be assessed in different ways. Blanckenhorn *et al.* [17]
150 compared latitudinal clines in body size between the sexes and obtained different results

151 depending on whether they examined clines in size ratios between the sexes (ratio-clines),
152 or used an allometric approach plotting log body size of one sex versus that of the other.
153 We therefore compared results derived using ratio-clines and allometric methods. Firstly, we
154 determined the degree of difference between T-S responses of the con-specific males and
155 females (within single studies) as:
156
157 *T-S Ratio* = (larger T-S response / smaller T-S response) - 1 (1)
158
159 We defined the ratio as being positive when males had the greater T-S response, and
160 negative when females had the greater response. This formulation has an advantage of
161 providing symmetrical results around zero, regardless of which sex has the greater T-S
162 response.
163
164 Secondly, we utilized the commonly applied method of performing an RMA regression of the
165 $\log_{10}$ body size of one sex against the $\log_{10}$ of the other sex, where each individual data point
166 represents the paired size measurements at one of the experimental temperatures. This
167 allometric slope gives a quantitative expression of how the sizes of the sexes change
168 together. In this regression, the more size-responsive sex was represented on the y-axis and
169 the less size-responsive on the x-axis, so the slope was always ≥ 1. We subtracted 1 from
170 the slope and again defined the value as being positive when male size was the more
171 responsive, and negative when female size was the more responsive. This method once
172 again ensures that results vary around zero, and there is symmetry based on equivalent
173 differences between the sexes, regardless of which sex shows the greater response. We
174 term this slope value the RMA_{Index}; zero indicates isometry, i.e. equal covariation in male and
175 female size, while increasingly positive values indicate greater male size responses
176 (variation), and increasingly large negative values signify greater female size responses.
177

We quantified the absolute degree of SSD using the Sexual Dimorphic Index (*SDI*) of Lovich & Gibbons [33], where:

SDI = (mass of larger sex / mass of smaller sex) - 1 (2)

We followed the recent convention that the *SDI* index is given as a positive value when males are the larger sex, and as a negative value when females are larger. Mean mass values for each sex were predicted at 20^{o}C from the T-S regressions, which in most cases did not involve any extrapolation.

In order to compare estimates of sex differences in size responses to temperature derived using the two methods, we plotted each *T-S Ratio* value against its appropriate RMA_{Index} value across all 116 T-S responses and performed a Reduced Major Axis (RMA) regression (Figure 1). Additionally, we performed a paired Wilcoxon Signed-Rank test to compare *T-S Ratio* and RMA_{Index} values. To determine whether the proportion of male and female-biased *T-S Ratio* and RMA_{Index} values differed significantly from 0.5, we used a chi-squared proportionality test.

The independent effect of taxonomic order, environment type (terrestrial, freshwater, marine) and life cycle type (i.e. hemi- vs. holometaboly) on the size and sign of the *T-S Ratio* and RMA_{Index} was determined using analysis of variance. Crustaceans were considered hemimetabolous, as these have direct development from larvae to juveniles to adults. *Post-hoc* comparisons (TukeyHSD) were used to identify any significant differences in both the *T-S Ratio* and RMA_{Index} between taxonomic orders. Ordinary least squares (OLS) regression analysis was used to determine whether the *T-S Ratio* changes significantly with the absolute degree of sexual size dimorphism (indexed by *SDI*). All statistical analyses, with the exception of RMA analyses, were conducted using the free statistical software package *R*

205 [34]. All RMA analyses were performed using the free statistical program *RMA for JAVA*
206 *v.1.21* [35].
207
208 To quantitatively assess the degree to which absolute sizes of males and females converge
209 or diverge at increasing temperatures, we determined sex-specific slopes of the linear
210 regressions of dry mass (mg) on temperature for each sex (as an estimate from what may
211 be a somewhat curved relationship). The difference between these slopes gives the degree
212 to which the two converge or diverge with increasing temperature; this difference was
213 expressed as a percentage of the female size (at 20°C), hence the formula is:
214
215 ([Slope for larger sex – slope for smaller sex] / mass of the female at 20°C)*100 (3)
216
217 A negative value represents convergence, and a positive value divergence with increasing
218 temperature. Normalizing to female mass at 20°C adjusts for any considerable differences in
219 absolute size between different taxa and the sexes. Again, we used analysis of variance to
220 determine the effect of the absolute degree of SSD (indexed by *SDI*) and taxonomic order on
221 change in absolute size difference with temperature, and a *post-hoc* Tukey HSD test to look
222 for significant differences between individual taxonomic orders. In addition, a series of one-
223 sample *t*-tests were used to identify which orders, if any, had a mean change in absolute
224 size difference between sexes with temperature that differed significantly from zero.
225
226 **Results**
227 Our meta-analysis includes 116 paired male and female T-S responses [% change in dry
228 mass (DM) $°C^{-1}$] from 85 arthropod species, including representatives from 17 taxonomic
229 orders from marine, freshwater and terrestrial environments. These responses have a
230 negative slope in ~84% of cases, and only in 2 instances was the sign of the T-S response
231 different between males and females within a species. There is wide variation in the strength
232 and direction of the T-S response, ranging from -8.15%$°C^{-1}$ to 5.67%$°C^{-1}$ in females. This

variation across species can be largely accounted for by strong differences in responses between water-living versus air-breathing species [22,23], and, in terrestrial arthropods, between univoltine and multivoltine species [23].

In comparing the two methods used to assess which sex has the stronger size response to warming (*T-S Ratio* vs. RMA_{Index}) (Figure 1), we typically find a close agreement between them. The RMA_{Index} suggests male body size is more responsive to temperature in 61 of 116 cases, which compares with 64 cases calculated using the *T-S Ratio*. Only in 11 instances did the two disagree on which sex had the greater size response to temperature. Regressing the two metrics against one another (using RMA) (Figure 1), and excluding the two extreme values indicated in brackets, gives a slope of 1.25 (1.13 to 1.38, 95% CI range) and an intercept of 0.06 (-0.03 to 0.15, 95% CI range). This slope is significantly different from 1, while the intercept is not significantly different from zero, as inferred from the 95% confidence intervals (Figure 1). Including the two extreme values also results in a slope significantly greater than 1 (slope =2.71, 2.25 to 3.16, 95% CI range). Comparing the *T-S Ratio* and RMA_{Index} values using a paired Wilcoxon Signed-Rank test also reveals *a* significant difference between the two (V=3295, p=0.01). We conclude that although the two metrics produce on average very similar values, the *T-S Ratio* tends to give somewhat more extreme values than does the RMA_{Index}. Because of the very close similarity in the results between these methods, we only present the *T-S Ratio* data henceforth. However, all analyses have also been undertaken using the RMA_{Index} and are summarised in the Supplementary Information: these further support the conclusions we present here.

We observe similar body size plasticity to temperature in both the males and females of a species on average. We find a significant correlation between female and male T-S responses across species ($p<0.001$, $R^2=0.81$), with an RMA regression slope of 1.09 (1.00-1.18, 95% CI range), and with an intercept of 0.38 (0.13-0.63, 95% CI range) (Figure 2). We find that male size responds to temperature more strongly than size of con-specific females

261 in 64 of 116 cases, as assessed using the *T-S Ratio*. Hence, the null hypothesis that a
262 stronger size response is observed equally often in each sex cannot be rejected (chi-
263 squared proportionality test; χ^2=1.24, p=0.27). This finding is further supported when size
264 response is measured using the RMA_{Index} (χ^2=0.22, p=0.64), in which male size responds
265 more strongly than conspecific female size to temperature in 61 of 116 cases.
266
267 Our analysis highlights a close similarity in the T-S responses of both sexes within the
268 Arthropoda, and also within orders of Arthropoda (Figure 3), although some orders have
269 much fewer data than others in our study. Although within single taxonomic orders there is
270 variation in the *T-S Ratio* between species, analysis of variance and *post-hoc* comparisons
271 (Tukey HSD) show taxonomic order to have no significant effect on the size or sign of the *T-*
272 *S Ratio* ($F_{17,98}$=0.77, p=0.72), and there appears to be no systematic patterns, such that in all
273 orders for which we have sufficient data to make the test, the mean value does not differ
274 significantly from zero (Figure 3). Similarly, we find no effect of environment type (marine,
275 freshwater, terrestrial) on the thermal dependence of SSD ($F_{2,113}$=2.41, p=0.09), even though
276 we know overall size and sign of T-S responses shown by animals relates strongly to these
277 different environmental categories [22]. The effect of life cycle (hemi- vs. holometaboly) was
278 also non-significant, both when testing across the entire dataset ($F_{1,114}$=0.16, p=0.69) and
279 exclusively within insects ($F_{1,92}$=0.47, p=0.49). Although the *T-S Ratio* values for Orthoptera
280 do not differ significantly from zero, in all 6 species considered female size responded
281 (increased) most to warmer rearing temperatures (Figure 3).
282
283 The *T-S Ratio* does not change significantly with the degree of SSD (as indexed by *SDI*),
284 inferred from the non-significant OLS regression between the two ($F_{1,114}$=0.28, p=0.60).
285 Thus, across environments, orders, and for varying degrees of *SDI*, we find no evidence to
286 suggest greater thermally induced variance in male size (i.e. no evidence to support an intra-
287 specific version of Rensch's rule) or indeed the opposite, greater variance in female size.

Neither sex exhibited significantly greater relative body size response to temperature than the other on average.

Warmer rearing conditions cause male and female absolute sizes to converge in 62 cases, and diverge in 54 cases. We find a significant positive relationship between the extent of convergence/divergence in body size with warming and the strength of the female T-S response, such that species which exhibit a strong negative T-S response also show the greatest convergence in absolute body size with warming, whilst those that exhibit a strong positive T-S response show the greatest divergence in absolute body size with warming ($F_{1,113}$=98.2, p<0.001, r^2=0.46). The corresponding regression lies predominantly within the range of values predicted given the range in *SDI* observed across our dataset, and based on an assumption that both males and females have identical proportional T-S responses (see Figures S2a and S2b in our Supplementary Information for a conceptual and quantitative examination of this). This leads us to the simple explanation that this strongly significant relationship is an outcome of similar T-S responses between males and females, which leads to greater absolute degree of size convergence and divergence the greater the relative response; an outcome expected simply from mathematics, but one with possible ecological implications. Taxonomic order has no significant effect on convergence or divergence ($F_{16,99}$=1.51, p=0.11), and the mean degree of size convergence or divergence does not differ significantly from zero, with the exception of three orders: Cyclopoida (-1.94% $°C^{-1}$ ±1.28CI; t_4=-4.20, p=0.01), Diptera (-0.24% $°C^{-1}$ ±0.19CI; t_{37}=-2.58, p=0.01) and Orthoptera (4.61% $°C^{-1}$ ±2.47CI; t_5=4.79, p<0.01) (Figure 4). Hence there is strong divergence in the absolute size of the sexes with warming in Orthoptera, but convergence in the Cyclopoida and Diptera.

Discussion

In our examination of the T-S responses of a wide range of arthropod species we find that male size responds to temperature more strongly than size of con-specific females in 64 of

116 cases, as assessed using the *T-S Ratio* (Figure 2). We cannot statistically reject the null hypothesis that a stronger size response is observed equally often in each sex. Indeed, this finding is also supported when size response is measured using the $RMA_{Index.}$ Furthermore, our analysis highlights a close similarity in the T-S responses of both sexes within orders of Arthropoda (Figure 3). However, we must highlight that our conclusions are phylogenetically limited, in that only 5 orders (Diptera, Orthoptera, Lepidoptera, Coleoptera and Calanoida) included 6 or more data sets, while most orders (11 of 17) were represented by just 3 or fewer. Moreover, orders for which there are more data are still taxonomically restricted. For example, the majority of dipteran species are from just two families (Drosophilidae and Culicidae), while >50% of lepidopteran species are from two families (Lycaenidae and Nymphalidae), though these two butterfly families have the greatest number of species worldwide.

Although there is a considerable range of T-S responses, from a large increase in size with warming (especially large bodied univoltine terrestrial species), to marked reductions in size with warming (in many large-bodied aquatic species) (see Horne *et al*. [23]), we find no systematic sex-based differences in response size within arthropods. This outcome occurs despite the often radically different behaviour, physiology, life-history and body size between the sexes [36-38]. Furthermore, the average lack of sex differences in the T-S response also appear to be unaffected by the large variation in the degree of SSD, or taxonomic order. Finally, the *T-S Ratio* does not significantly correlate with the absolute degree of SSD (indexed by *SDI*), which contrasts with the findings of Teder & Tammaru [13], in which females typically showed stronger phenotypic plasticity responses with varying environmental quality when SSD was more female-biased.

Blanckenhorn *et al*. [17], in an analysis which included both vertebrates and invertebrates, examined latitudinal clines in male and female body size, and found somewhat contradictory outcomes depending upon the form of analysis used. Similar to the approach employed

here, they calculated both an RMA regression of the size of one sex against the other, as well as comparing the ratio of latitudinal size clines of each sex (termed slope ratio). Male size was found to vary more than female size in 66 of 98 species when examining data sets based on latitudinal-size gradients. Thus, intra-specifically the results conformed to greater male size variation (RR), suggesting a connection between Bergmann's and Rensch's rules. However, when using a conventional RMA regression, Blanckenhorn *et al.* [17] found that the size of neither sex was significantly more variable than the other (male size was found to vary more than female size in 55 of 98 species). Notably, in both their study and our own, regressing the *T-S Ratio* (or slope ratio) against the RMA_{Index} generates a slope significantly greater than 1, suggesting that the former produces the more extreme values of the two metrics. This statistical effect has not manifested itself to the same extent in our own study. We note that because the T-S response of the less variable sex can be zero (i.e. the denominator in the T-S ratio equation), the T-S Ratio can be infinite. A very low denominator value compared with the numerator will also generate very large ratios, so generating large variability, hence the apparent contradiction that can occur between the two methods. Though the different results generated by these two metrics do not alter the major outcomes and conclusions presented here, they did lead Blanckenhorn *et al*. [17] to present contrasting findings between methodologies. Unlike Blanckenhorn *et al.* [17] we find no significant differences in the body size responses of males or females, regardless of whether we use the RMA_{Index} or *T-S Ratio*. We note that whilst T-S responses are measured in controlled laboratory conditions using individuals from the same population, a great variety of influences can potentially select for changes in SSD across latitudes, which may not necessarily be linked directly with temperature. These factors may include, but are not limited to, the increased likelihood of genetic variation between populations, as well as size-dependent mortality and environmental factors such as food and season length.

The contrasting proximate mechanisms by which T-S responses are generated in organisms [39], and the extent to which the magnitude and direction of these responses correlate with

life history (voltinism) [23], with a possible trade-off between numbers of generations in a year and size at maturity, leads to the suggestion that these responses relate to fitness and hence are adaptive. Further, as the thermal dependence of size at maturity is so similar (in relative terms) between the sexes in individual species, then the responses may have similar fitness costs and benefits in both males and females. While it is conceivable that a very high genetic correlation between the sexes of a species may help explain the similar size response of males and females to temperature [40], this potential constraint seems to be overridden in cases of other environmental factors (e.g. changed diet or juvenile density) that generate systematic differences in size responses between males and females [19] (see Table 1).

The contrast between lack of effect of temperature on SSD observed here and the systematic effect of food quantity and also larval competition on SSD in insects [13,19], implies that there is generally a sex-dependent effect on body size caused by food resources but not by temperature (see Table 1 for a quantitative comparison of the degree of plastic variation in the sexes with changes in different environmental conditions). A useful distinction is whether food supply or quality, or increased competition, acts primarily on reducing the size of the larger sex, which is consistent with energetic restrictions acting to a greater degree on larger bodies, or whether it acts primarily on just females, even in species in which males are the larger sex (e.g. some odonates). Female size was usually affected most by food supply, but in the few species with larger males than females, no consistent sex-dependent size response was observed [13]. Thus, the relative contribution of sex versus body size to the degree of size plasticity was not clearly distinguished.

The metrics used to study the allometric scaling of SSD commonly examine relative (proportional) change in body size (e.g. Blanckenhorn *et al*. [17]). Here, we also used two methods that examine change in relative body size within species, and which account for differences in size between species. In both cases we obtained the same major conclusions.

In contrast to these quantitative analyses of relative size change, analyses of absolute size differences between sexes of conspecifics, and how these respond to environmental factors, has received much less attention. Yet measuring the extent to which increased rearing temperature causes absolute body sizes to converge or diverge between the sexes may be biologically informative. For example, females are very commonly the larger sex in arthropods [19,41]: yet if both sexes show similar negative T-S responses (using the metrics described herein), then their absolute body sizes will converge with increasing temperature.

We observe considerable variation in both convergence and divergence in absolute mass across species that exhibit both a normal and converse TSR (represented conceptually and quantitatively in supplementary Figures S2a and S2b respectively). Within the Orthoptera, absolute body sizes of the sexes significantly diverge with warming (Figure 4). This divergence arises partly from the fact that Orthopterans generally follow the converse TSR [23] and have larger females than males, so that a similar T-S response of males and females will cause divergence in absolute size between the sexes with warming (a similar proportional size increase in the larger sex makes the absolute difference greater). But in addition, although the mean *T-S Ratio* value for this order is not significantly different from zero (Figure 3), in all 6 orthopteran species the females have a stronger *T-S ratio* than conspecific males (Figure 3). The relatively strong variation in female body size with temperature observed in Orthoptera exerts an important influence on the mean *T-S Ratio* and RMA_{Index} of species that follow the converse TSR. Specifically, when comparing the thermal dependence of SSD between species that follow either the normal or converse TSR, we observe that females are the more variant sex in species that increase their size with warming, whilst there is no significant difference between the sexes in those that exhibit a normal T-S response. We report these observations with caution; Orthoptera account for nearly a third of positive T-S responses in our dataset, for which the sample size is already comparatively small (n=19 for positive T-S responses vs. n=97 for negative T-S responses). Indeed, we find no significant difference in body size sensitivity between the sexes in either

group when Orthoptera are excluded. Orthoptera have strongly positive T-S responses and strongly negative latitude-size clines, with larger species often being univoltine, and hence potentially affected by season-length constraints on size-at-maturity [23], especially in the larger sex, which typically reaches adulthood later [42,43]. If such constraints are indeed greater in the larger sex (more season-length constrained sex), warming may favour increased body size especially in females, hence the strong divergence in orthopteran absolute body sizes between the sexes at increased rearing temperatures. When there is more data available, an analysis of whether these sex-based patterns in thermal body size sensitivity extend more generally to other large univoltine species would be particularly informative.

A potential selection pressure is to reduce extreme size-divergence if it can lead to incompatibility between the sexes. Could such selection lead to very similar absolute changes in size between the sexes? In a species of Jerusalem cricket (Orthoptera: Stenopelmatinae: *Stenopelmatus*) copulatory-size incompatibility was observed even when the male was as little as 2mm longer than their conspecific female, resulting in misalignment that prolonged or completely impeded copulation [31]. The absolute difference in mass or specific body lengths between the sexes can impact many size-dependent mating and reproduction events, including courtship, mate choice, copulation, mating behaviours, and success of offspring when parental care is shared. The fact that many studies on size dimorphism focus on a single linear dimension of body size or total mass may be problematic to interpretation if critically important body dimensions do not change isomorphically to one another [18].

In conclusion, while previous comparisons of plastic body size responses of the sexes in relation to larval density and food quality in insects find greater relative variation in female size, especially when females are the larger sex [13,19], we find that plastic temperature-size responses under excess food shows no consistent inter-sex differences in size

456 response on average when examined across a wide range of arthropod orders. Indeed, our
457 more comprehensive analysis for this variable concurs with the lack of consistent
458 temperature effect on SSD detected by Stillwell *et al*. [19]. Consequently, we propose that in
459 arthropods, temperature, unlike food supply, does not consistently affect optimal body size of
460 one sex more than the other.
461
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471

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583 **Figure legends**

584 **Figure 1**. Comparison of two methods for estimating sex differences in body size response
585 to rearing temperature: *T-S Ratio* [(larger response % change in body mass $^{o}C^{-1}$ / smaller %
586 change in body mass $^{o}C^{-1}$)-1] and RMA_{Index} [slopes derived from the RMA regression of body
587 mass values for the sex with the more thermally responsive body size on the y-axis (logged)
588 versus the body size values for the less responsive sex on the x-axis (logged) minus 1] for
589 arthropod species, where each point represents a single species in a single study. Positive
590 values represent greater response in male size than female, negative values greater
591 response in female size. An RMA regression through the data (excluding the two extreme
592 ratios given in brackets) is given by the solid line, and has a slope of 1.25 (1.13-1.38, 95% CI
593 range). The RMA slope is significantly different from 1. The diagonal dashed line indicates a
594 1:1 relationship. The number of values falling within each of the four quadrants (*n*) is
595 indicated.
596
597 **Figure 2**. Female versus male T-S responses (% change in body mass $^{o}C^{-1}$). Each point
598 represents a single study of a species and is classified by taxonomic order. An RMA
599 regression through the data is given by the solid line, and has a slope of 1.09 (1.00-1.18,
600 95% CI range) with an intercept of 0.38 (0.13-0.63, 95% CI range), denoted in the inset
601 panel by the black and open circles respectively. The RMA slope is not significantly different
602 from 1. The diagonal dashed line indicates a 1:1 relationship.
603
604 **Figure 3**. A comparison of the thermal dependence of male and female size responses (*T-S*
605 *Ratio*) within arthropod species, categorised by taxonomic order. Error bars denote 95% CI.
606 The vertical dashed line denotes zero, i.e. no difference between male and female body size
607 responses to temperature. Values greater than zero indicate more responsive male mass.
608 Values less than zero indicate more responsive female mass. All order-specific *T-S Ratios*
609 do not differ significantly from zero. The percentage of cases in which female size was the

610 more responsive is given in brackets on the left hand side of the panel after each order. The
611 sample size (*n*) of each order is given on the right hand side of the panel.
612
613 **Figure 4.** Change in the absolute mass difference between the sexes of a species with
614 increasing temperature, expressed as a percentage of the female size (at 20°C) per degree
615 Celsius. Data are categorized by taxonomic order. The overall effect of taxonomic order on
616 the degree of convergence or divergence is not significant ($F_{16,99}$=1.51, p=0.11). The mean
617 for each order does not differ significantly from zero, with the exception of Cyclopoida (-
618 1.94% °C^{-1} ±1.28CI; t_4=-4.20, p=0.01), Diptera (-0.24% °C^{-1} ±0.19CI; t_{35}=-2.24, p=0.03) and
619 Orthoptera (4.61% °C^{-1} ±2.47CI; t_5=4.79, p<0.01). These orders are marked with an asterisk
620 (*) and + or – to indicate these have divergence or convergence respectively.

Table 1. Comparison of sex-specific plasticity in body mass in relation to environmental variables. We followed the methodology of Stillwell *et al.* (2010) [19] for the T-S data, such that $\log_{10}$ male size is plotted on the y-axis, and $\log_{10}$ female size on the x. Hence when the RMA slope is <1 females are the more size responsive sex, and when the RMA slope is >1 males are more size responsive. CV is the coefficient of variation of body size across the data within each study. Asterisks denote a significant difference between the sexes, where * gives $p<0.05$, and ** gives $p<0.01$. Table modified from Stillwell *et al*. (2010) [19], with additions from this study.

Environmental Variable (Taxonomic group)	**Which Sex is More Plastic**			**Average degree of plasticity (CV among environments)**			**Source**
	Females (No. studies with RMA slope < 1)	**Males (No. studies with RMA slope > 1)**	X^2	**Female**	**Male**	***t***	
Temperature (Arthropoda)	55 (47.4%)	61 (52.6%)	0.22	12.3%	12.1%	0.41	This Study
Temperature (Insecta)	46 (48.9%)	48 (51.1%)	0.01	11.6%	11.0%	1.14	This Study
Larval density / larval competition / diet quantity (Insecta)	18 (72.0%)	7 (28.0%)	4.84*	16.0%	12.2%	3.42**	Stillwell *et al*. (2010)
Pathogenic infection (Insecta)	3 (50.0%)	3 (50.0%)	0.00	6.9%	7.2%	0.34	Stillwell *et al*. (2010)
Photoperiod (Insecta)	1 (16.7%)	5(83.3%)	2.67	8.6%	10.7%	2.18	Stillwell *et al*. (2010)
Diet Quality (Insecta)	83 (61.9%)	51 (39.1%)	7.64**	12.5%	11.5%	2.47*	Stillwell *et al*. (2010)

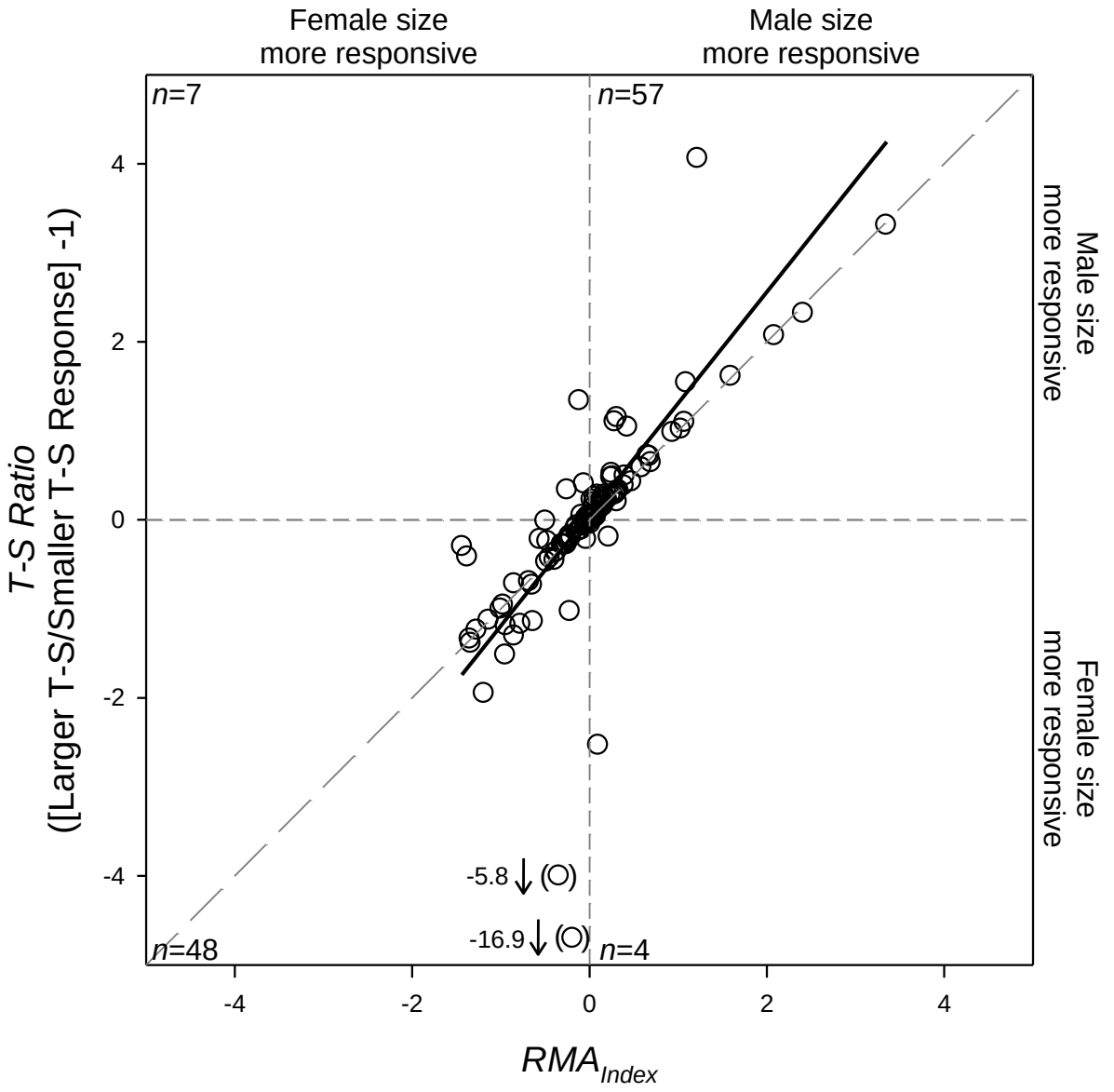
Female size
more responsive
Male size
more responsive
n=7
n=57
n=48
n=4
-5.8
-16.9
T-S Ratio
([Larger T-S/Smaller T-S Response] -1)
RMA Index
([Slope Of More Variant Sex vs. Less Variant Sex] -1)
Male size
more responsive
Female size
more responsive

Figure 1

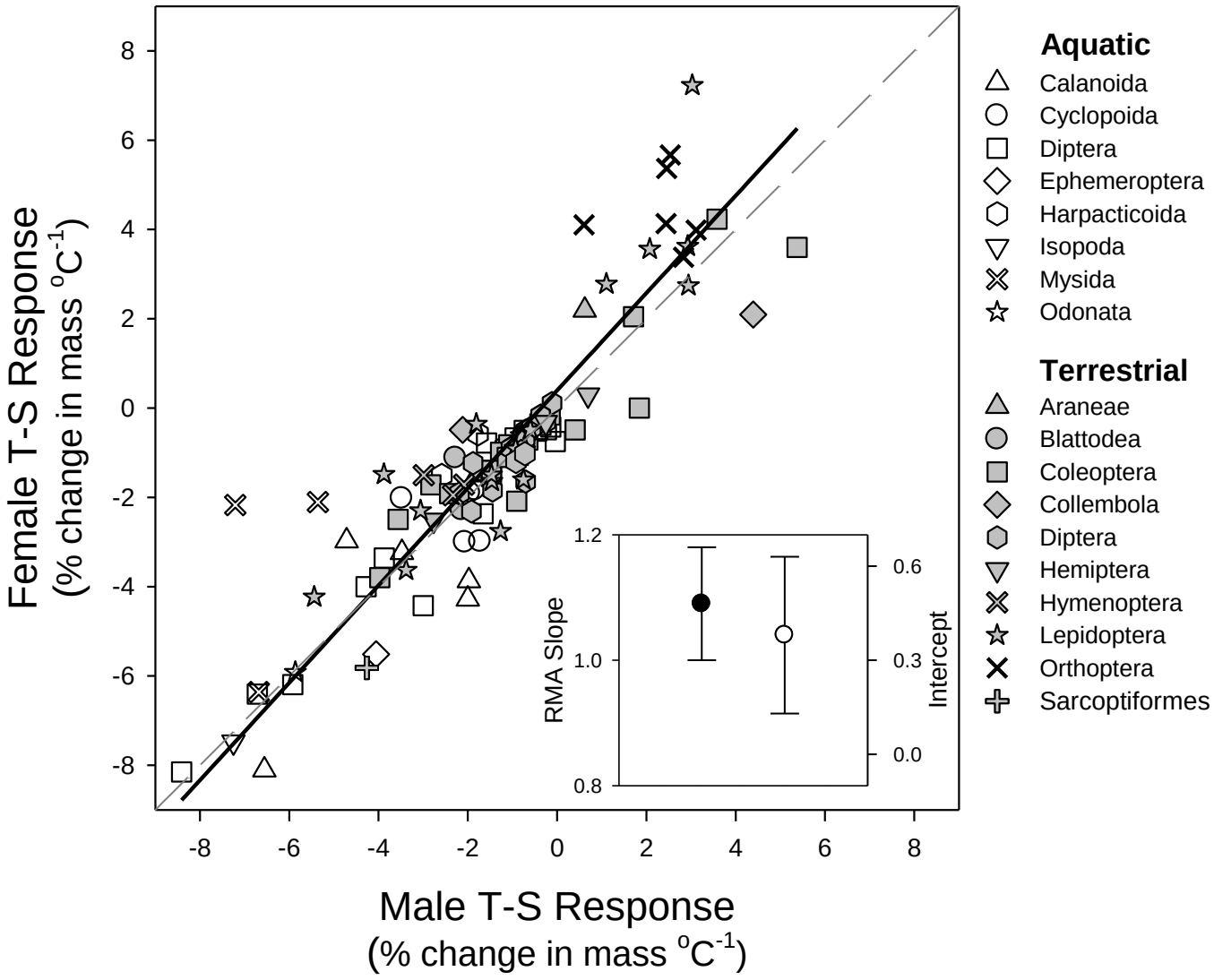
Female T-S Response
(% change in mass °C-1)
Male T-S Response
(% change in mass °C-1)
RMA Slope
Intercept
Aquatic
Calanoida
Cyclopoida
Diptera
Ephemeroptera
Harpacticoida
Isopoda
Mysida
Odonata
Terrestrial
Araneae
Blattodea
Coleoptera
Collembola
Diptera
Hemiptera
Hymenoptera
Lepidoptera
Orthoptera
Sarcoptiformes

Figure 2

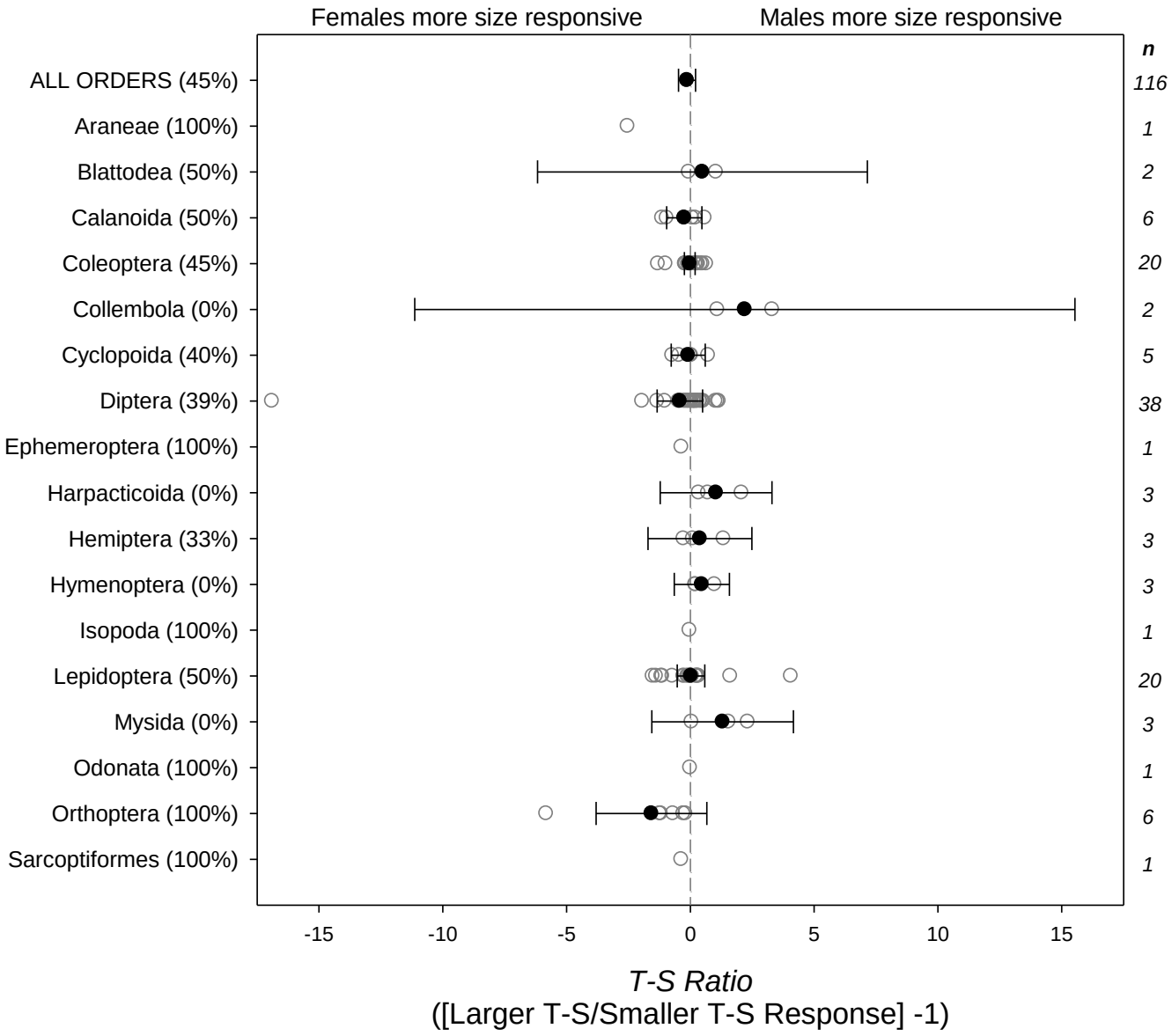
Females more size responsive
Males more size responsive
n
ALL ORDERS (45%)
Araneae (100%)
Blattodea (50%)
Calanoida (50%)
Coleoptera (45%)
Collembola (0%)
Cyclopoida (40%)
Diptera (39%)
Ephemeroptera (100%)
Harpacticoida (0%)
Hemiptera (33%)
Hymenoptera (0%)
Isopoda (100%)
Lepidoptera (50%)
Mysida (0%)
Odonata (100%)
Orthoptera (100%)
Sarcoptiformes (100%)
116
1
2
6
20
2
5
38
1
3
3
3
1
20
3
1
6
1
-15
-10
-5
0
5
10
15
T-S Ratio
([Larger T-S/Smaller T-S Response] -1)

Figure 3

Change in absolute size difference between the sexes with temperature (expressed as % female mass °C-1)
10
5
0
-5
-10
32.4
Sexes diverge in absolute size with warming
Sexes converge in absolute size with warming
Calanoida
Cyclopoida
Sarcoptiformes
Mysida
Isopoda
Araneae
Diptera
Ephemeroptera
Coleoptera
Lepidoptera
Blattodea
Harpacticoida
Hemiptera
Collembola
Odonata
Hymenoptera
Orthoptera
Taxonomic Order

Figure 4